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Similarities and Contrasts in the Local Insect Faunas Associated with Ten Forest Tree Species of New Guinea[1]

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ABSTRACT: Insect faunas associated with 10 tree species growing in a submontane area in Papua New Guinea are described and compared. In total, 75,000 insects were collected on these trees during the day and night by hand collecting, beating, branch clipping, intercept flight traps, and pyrethrum knockdown over a 1-yr period. Association of chewing insects with the hosts was inferred from feeding trials. Characteristics of the fauna associated with each tree species are briefly outlined, with an emphasis on chewing insects. Four subsets of data, of decreasing affinity with the host, were analyzed by canonical correspondence and cluster analyses: (1) specialist leaf-chewers, (2) proven leaf-chewers, (3) all herbivores (including transient leaf-chewers and sap-suckers), and (4) all insects (including nonherbivore categories). Analyses of similarity between tree species were performed using number of either species or individuals within insect families. Analyses using number of individuals appeared more robust than those using number of species, because transient herbivore species artificially inflated the level of similarity between tree species. Thus, it is recommended that number of individuals be used in analyses of this type, particularly when the association of insects with their putative host has not been ascertained. Not unexpectedly, the faunal similarity of tree species increased along the sequence (1)–(2)–(3)–(4). Convergence or divergence in faunal similarity among tree species certainly results from many factors. Among those identified, successional status (which can be related more generally to the type of habitat in which the host grows) appeared important for specialist leaf-chewers; gross features of the host, such as leaf palatability and leaf weight (related to leaf toughness), were important for leaf-chewers; features presumably influencing insect flight and alighting (leaf area, probably related to foliage denseness) seemed be important for all herbivores; and features related to host architecture (tree height, type of bark) were important for all insects. Taxonomic isolation and phylogeny of trees were clearly unrelated to faunal similarity, even for specialist leaf-chewers. We discuss briefly from a conservation perspective the loss of tree species in our system and the outcome for associated insect faunas.

IN SOME INSTANCES, a close correspondence between the faunal similarity of insect herbivores and the taxonomic affinity of their herbaceous host plants has been demonstrated (e.g., Berenbaum 1981). Trees usually offer a much more complex set of habitats for insects than herbaceous plants, both in terms of plant architecture (e.g., Lawton 1983) and of genetic variability (e.g., Whitham and Slobodchikoff 1981). As a result, trees often support a much more diverse insect fauna than herbs (Lawton and Schröder 1977). This, in turn, may explain why (diffuse coevolution: see Fox 1981) faunal similarities in trees

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often do not reflect their taxonomic affinities (e.g., Futuyma and Gould 1979, Scriber 1988, Holloway 1989, Cytrynowicz 1991; but see Holloway and Hebert 1979). In addition, trees frequently also support a rich nonherbivore fauna of predators, parasitoids, wood-eaters, fungal-feeders, and scavengers (Moran and Southwood 1982).

Although we can expect biogeographical and historical factors (accounting for host biochemistry and geographical distribution) to shape in a similar way the insect faunas associated with host trees of close taxonomic affinity and history, numerous other factors may decrease or increase the congruence between faunal similarity and host phylogeny. These factors, which are discussed at more length by several authors (e.g., Lawton and Schröder 1977, Kennedy and Southwood 1984, Nicolai 1986, Cornell and Kahn 1989, Jones and Lawton 1991, Basset 1991, Basset and Burckhardt 1992), fall in three main categories: (1) local variables such as mesoclimate and local productivity; (2) host-related variables less directly related to host phylogeny (however, in some cases, this can be debated) such as tree phenology, shape, size, toughness and hairiness of leaves, denseness of foliage, local abundance and height of tree, and complexity of the bark; (3) the intrinsic composition of the fauna and, in particular, the identity of the dominant herbivores, which, in turn, is likely to influence the suite of main predators and parasitoids.

Most of these findings derive from the study of temperate tree species and their insect associates. Patterns of insect distribution on tropical tree species are much less understood. In one of the few studies addressing this issue, Stork (1987a) reported that taxonomic similarity of the trees, the distance between them, and their epiphyte load were important variables determining the faunal similarity of Bornean rain forest trees. Many past and current investigations of arboreal insect faunas (e.g., Erwin and Scott 1980, Stork 1987a) used pyrethrum knockdown to collect a large number of insects rapidly. The specimens collected in those conditions were, most often, dead (but see Paarmann and Stork 1987). As a result, it is often difficult to ascertain whether insect herbivores collected do actually feed on the tree species sampled. Recently, Moran et al. (1994) questioned whether the lack of information about the closeness of association between herbivorous insects and their putative hosts was confusing our understanding of insect distribution on tropical trees. Other alternatives, which could help in resolving this uncertainty, to "snapshots" of insect communities obtained with pyrethrum knockdown include repeated fogging of the same tree species along altitudinal gradients or different locations (e.g., Allison et al. 1993), careful long-term surveys of many potential hosts (e.g., Marquis 1991), and feeding trials and rearing of live specimens collected with different techniques (e.g., Basset 1992, 1994).

Studying the faunal similarity of tropical trees may be important both for a better understanding of food-web ecology in tropical forests and for their biological conservation. For the latter, it can result in important implications for management of tropical forests. For example, if most of the tree species support very different insect faunas, then the percentage loss of species will approach the percentage loss of area by, for example, logging (e.g., Mann 1991).

There are various ways to report faunal similarity between different host trees. For example, it is equally, if not more, interesting to investigate why tree species A supports more species/individuals of, say, Geometridae than tree species B, compared with investigating why species Z of Geometridae is present on tree species A but not on tree species B. Note that these two questions may be related, but not necessarily. In this contribution, we focus on the first approach and explore broad patterns of insect similarity among 10 tree species in New Guinea at the familial level and the reasons for convergence or divergence in faunal similarity. Our sampling protocol enabled us to ascertain the closeness of association between leaf-chewers and their putative hosts. Consequently, our analyses of faunal similarity could be performed with particular reference to the closeness of association between insects and hosts, using the following sequence: specialist leaf-

chewers, ascertained leaf-chewers, all herbivores (including transient leaf-chewers and sap-suckers), and all insects (including non-herbivore groups). As an introduction to our analyses of similarity, we briefly characterize the insect fauna associated with each tree species studied.

MATERIALS AND METHODS

Study Site and Study Trees

Sampling was performed on the slopes of Mount Kaindi, near and within the grounds of the Wau Ecology Institute, Wau, Papua New Guinea (7° 24′ S, 146° 44′ E). Altitude of collecting ranged from 1100 to 2362 m (summit), but was mostly confined to 1200–1400 m. Mount Kaindi has been cleared locally, leaving a mosaic of grasslands and forest patches, dominated by secondary forest (Valkenburg and Ketner 1994). The main forest formations encountered on the slopes include lower and midmontane rain forest (Johns 1982). The climate is "humid to perhumid mesothermal with little or no water deficit" (McAlpine et al. 1983). The study area was further detailed by Gressitt and Nadkarni (1978) and Valkenburg and Ketner (1994).

Ten woody plant species (native forest trees and shrubs) were studied. Criteria for choosing these species included (1) they were common within the Mount Kaindi area; (2) they were representatives of 10 different plant families; and (3) they included species of different successional stage, different leaf production patterns, and different height. Hereafter, they are designated by their generic names.

Insect Collecting

Insects were collected by Y.B. from the foliage of the study trees by hand collecting, foliage beating, branch clipping, intercept flight traps, and pyrethrum knockdown. The first four of these methods were used during both day and night, whereas pyrethrum knockdown was only performed during the day, in early morning. Living specimens from the first three methods were used in feeding trials (see next section). Hand collecting and foliage beating represented, for each tree species, about 50 hr of hand-collecting activity and 300 beating samples distributed among different individual trees. Branch clipping represented, for each tree species, 55 samples of about 33 m^2 of leaf surface, obtained from different individuals. One intercept flight trap (as described in Springate and Basset 1996) was set up in the middle of the crown of one individual of each tree species. The trap collected insects continuously throughout 1 yr and was surveyed approximately every 11 days. One individual of each tree species was sampled using pyrethrum knockdown [solution of 5% Pyranone (Fairfield American Corp., Rutherford, NJ) and kerosene], using from 12 to 20 trays (each 1 m^2 of surface), depending on tree size (total: 159 trays used for all tree species). The protocol of Allison et al. (1993) was followed with the only difference being that trees were fogged by climbing directly into them, not from an adjacent tree.

Active sampling was performed from February to July 1992 and from November 1992 to April 1993; traps were run from April 1992 to April 1993. Field data have thus been gathered over more than a year and take into account the seasonal variation in insect diversity and abundance at the Wau site. When the foliage could not be sampled from the ground, the single rope technique provided access to the crowns (Perry 1978). Sampling effort was the same for each tree species, and all material thus derived has been considered for subsequent analyses.

Because knowledge of the ecology of most Papuan insects is fragmentary, specialization of adult insects had to be assessed from feeding trials in the laboratory. Live insects were stored in plastic vials at room temperature and in conditions of near-saturated relative humidity. The insects were provided with fresh foliage of the tree species from which they were collected until they died or accepted food. In the latter case, they were then tested in random order for 24-h periods on

the foliage of the nine other study species. Feeding damage was scored visually, relative to insect body size, on a logarithmic scale, as follows: 0, no feeding; 1, attempting to feed; 10, moderate feeding; 100, extensive feeding. This procedure emphasized regular feeding as contrasted to food probing. Insects were assigned to four leaf-feeding categories according to the results of the feeding tests: (1) "specialists" (i.e., insects tested on three or more plant species but fed only on the plant they were collected from [sum of feeding scores <100]); (2) "generalists" (i.e., insects tested on three or more plant species and fed on two or more plants belonging to different plant families [sum of feeding scores ≥ 100]); (3) "unknown specialization" (i.e., insects that, because of death, could not be tested on more than two plant species); and (4) "incidentals" (i.e., insects that did not feed in the trials). Together, categories 1, 2, and 3 are referred to as "proven feeders." Leaf-chewers that were collected dead (by the traps and pyrethrum knockdown) were labeled as "additionals." Species of Cerambycidae that fed on foliage or on shoots for maturation feeding were also included in the chewing category and tested in feeding trials. The procedure is further detailed and discussed elsewhere (Basset 1994, Basset and Samuelson in press).

Resolution of Sorting

Although a wide range of arthropods was collected from the foliage of study trees, the analyses focused on insects. Information about Acari is not detailed here because their small size and the sampling protocol used increased the probability that their abundance and species richness was underestimated. Araneae were counted but not sorted to families. As far as possible, the insect material was sorted to families, except Psocoptera and imagines of Lepidoptera. The latter, collected in alcohol, were difficult to study.

A higher resolution of sorting was adopted for insect herbivores. Sap-sucking species were assigned to morphospecies on the basis of external characters, but not cross-checked among tree species. Furthermore, feeding on the tree species from which they were collected could not be ascertained. Coccoidea were not sorted to families. Chewing insects were assigned to morphospecies and cross-checked among tree species. For Lepidoptera, only mature larvae were assigned to morphospecies. As far as possible, caterpillars were reared to obtain adults and to refine morphospecies assignments. Adults of insect herbivores were later dry mounted at the Bishop Museum, Honolulu. Morphospecies assignment, hereafter "species" for sake of simplicity, was checked by G.A.S. (Coleoptera) and S.E.M. (Lepidoptera) and verified by specialists in many cases. In some cases, chewing species could be named, at least to genus. However, the protocol adopted in feeding trials resulted in the death of many caterpillars and lack of adults for identification. The material has been deposited in the collections of the Bishop Museum.

Statistical Methods

Our analyses focused on explaining similarities (or contrasts) among study trees in terms of the number of species or individuals within insect families, rather than studying the faunal overlap in terms of particular species present on study trees. This procedure was followed for the following reasons: we were interested in explaining broad patterns of insect similarity among study trees and the putative reasons for their resemblance or divergence; only part of the material (insect herbivores) was sorted to species cross-checked between trees; not all species of Lepidoptera could be cross-checked among study trees because of larval death; and analyses of patterns reflected by the overlap in presence or abundance of particular herbivore species are more likely to reflect patterns of foraging by generalist species than broad patterns in overall faunal similarity because study trees all belong to different plant families and the associated insect fauna is relatively specialized (see Basset 1994) (for an example dealing with foraging patterns of leaf beetles, see Basset and Samuelson in press).

Several multivariate techniques are avail-

able for analyzing similarity, particularly clustering and ordination. First, we performed canonical correspondence analysis (CCA), an ordination method that represents a direct gradient analysis (see Ter Braak [1986] for the interpretation of CCA diagrams and statistics). This allowed us to test whether certain qualities (variables) of the study trees were important in structuring similarities among tree species. The first step of the computations involved performing a correspondence analysis (CA). Second, we performed cluster analysis using the unweighted arithmetic average clustering method (UPGMA). This allowed us to account for the total variance in tree similarity, not just for that expressed in the few axes of the ordination (see Digby and Kempton 1987).

The matrices used in both types of analyses were either the number of species or the number of individuals within the most common insect families collected on each tree species. We performed the analyses for seven data sets (Table 2), grouped in decreasing order of affinity of taxa with the host tree as follows: (1) data relevant to leaf-chewing specialists only; analyses performed with the number of species and individuals; insect families were only included in the analyses if the total number of individuals collected was ≥ 3; (2) data relevant to proven leaf-chewers only; analyses performed with the number of species and individuals; in addition to families included in (1), other families were included if their total number of individuals was ≥ 3; (3) data relevant to herbivores only (including sap-suckers and incidental/additional chewers); analyses performed with the number of species and individuals; in addition to families included in (2), other families were included if their total number of individuals was ≥ 10; (4) data relevant to all insects (including nonherbivores); analyses performed with the number of individuals; in addition to families included in (3), other families were included if their total number of individuals was ≥ 15. For the analyses, Miridae and Phlaeothripidae were included in the nonherbivore fauna, because only some of these insects are probably truly phytophagous; the others are predators and/or fungal-feeders (e.g., Basset 1991).

CCA was performed using the program ADE 3.6 (Chessel and Dolédec 1993). CCA relates known variation in the environment to community composition. Ordination axes are chosen in the light of known environmental variables by imposing the extra restriction that the axes be linear combinations of environmental variables (Ter Braak 1986). Our environmental variables were related to host characteristics and differed for each data set. The choice of these variables followed the potential predictors of insect species richness on temperate trees (see references in the introduction), plus those that have been found of importance in the tropical system studied here (Y.B., unpubl. data). For data set 1, these variables included leaf water content, leaf palatability, total nitrogen content of mature leaves, successional status (pioneer or persistent), taxonomic isolation, and the number of young leaves recorded yearlong in branch-clipping samples. For data set 2, variables included leaf water content, leaf palatability, nitrogen, successional status, young leaves, and specific leaf weight, a measurement related to leaf toughness. For data set 3, variables included leaf water content, leaf palatability, mean leaf area, successional status, young leaves, and specific leaf weight. Eventually, for data set 4, variables included mean tree height, type of bark, mean leaf area, successional status, young leaves, and specific leaf weight. All variables and their measurements are detailed elsewhere (Basset 1994 and Y.B., unpubl. data), with the exception of bark type, which is listed in Table 1.

UPGMA is a clustering method routinely used in numerical ecology (e.g., Legendre and Legendre 1984). It was calculated with the program "R" of Legendre and Vaudor (1991). We used the coefficient of Kulczynski as a measure of similarity for these computations. This coefficient is particularly suitable for quantitative data, does not include double zeros, and does not give more weight to either abundant or rare taxa (Legendre and Vaudor 1991).

TABLE 1

SUMMARY OF RESULTS OF STUDY OF 10 TREE SPECIES

HOSTS	PLANT FAMILY	Status[a], H[b]	Ph[c]	B[d]	Sp[e]	Chw[f]	Tot[g]
Elmerrillia tsiampacca (L.) Dandy	Magnoliaceae	Pe, T	C	4	20	75	6,920
Cinnamomum cf. *culilaban* (L.) Presl	Lauraceae	Pe, S	I	4	37	212	6,974
Piper plagiophyllum K. Sch. & Laut.	Piperaceae	Pi, S	C	2	18	339	9,361
Ficus nodosa Teys. & Binn.	Moraceae	Pi, T	D	3	61	517	7,606
Pipturus argenteus Wedd.	Urticaceae	Pi, S	C	2	52	629	7,816
Castanopsis acuminatissima A. DC.	Fagaceae	Pe, T	I	4	94	408	8,936
Caldcluvia brassii Hoogl.	Cunoniaceae	Pi, S	C	2	39	454	4,699
Aleurites moluccana Willd.	Euphorbiaceae	Pe, T	C	1	25	111	8,839
Melicope denhamii (Seem.) T. Hartley	Rutaceae	Pe, S	I	2	36	335	7,449
Cordia dichotoma Forst.	Boraginaceae	Pi, T	D	4	45	262	7,136

[a] Successional status: Pe, persistent; Pi, pioneer.
[b] Average height when mature: S, <15 m; T, >15 m.
[c] Phenology of leaf production: C, continuous; D, deciduous; I, intermittent.
[d] Bark type (mature trees): 1, smooth, pale bark; 2, rugose, dark bark; 3, rugose, dark bark with some hollow branches; 4, scaly, rifted and dark bark.
[e] Number of associated chewing species recorded.
[f] Total number of individuals represented by these associates (CHW).
[g] Total number of insect individuals collected (TOT).

RESULTS

General Accounts of the Insect Faunas Associated with the Study Trees

In total, 75,736 and 2746 individuals of insects and spiders, respectively, were collected from the 10 study trees (Table 1). This material represented at least 199 insect families. Herbivore densities and the proportion of specialized leaf-chewers on each tree species are reported and discussed elsewhere (Y.B., unpubl. data). It is of interest to note that the contribution that leaf-chewers that feed on the study tree made to the overall insect fauna was rather low, between 1% (*Elmerrillia*) and 9% (*Caldcluvia*) of the individuals collected. This emphasizes trees as being habitats for a rich and diverse fauna, far from being restricted to herbivores.

Brief descriptions of the insect fauna associated with each tree species are summarized below, emphasizing abundance and species richness of insect families. Appendix 1 details the identity of the chewing species associated with each tree species, when known. For many insect species/genera, this constitutes the first ever host plant records. Appendix 2 lists the number of species and individuals of sap-suckers collected on each tree species, and Appendix 3 lists the number of individuals in the most common nonherbivore families collected on each tree species. In terms of number of individuals, the families listed in Appendices 1, 2, and 3 represented 65% of all individuals collected; the rest were mostly unassigned juvenile specimens, caterpillars too young to be assigned with certitude, and insect families of low occurrence. A very common species of Psyllidae, *Heteropsylla cubana* Crawford, which feeds on *Leucaena leucocephala* (Lamk) De Wit, contaminated the samples, irrespective of the sampling method used (see Appendix 2). This species, which was introduced to New Guinea in the 1980s (Muddiman et al. 1992), was not included in the analyses.

Elmerrillia. The herbivore fauna was poorly developed on this tree, with few specialist species among leaf-chewers, which were dominated by Lagriidae and Geometridae. Of interest is the record of several species of Papilionidae, whose status could not be ascertained and whose adults could not be reared. Cicadellidae, Derbidae, Pentatomidae, Lygaeidae, and Psyllidae were species-rich or abundant among sap-suckers. In particular, the free-living psyllid *Euryconus* sp.

attained relatively high densities and presumably was exploited by several predators and parasitoids, such as Coccinellidae, Cleridae, Miridae, Nabidae, Encyrtidae, and Hemerobiidae. Scavengers such as Blattellidae and Tenebrionidae were relatively common, along with Formicidae, which foraged mainly on the trunk and limbs of this large tree species.

Cinnamomum. Lepidoptera dominated the chewing guild on this tree (Geometridae and Tortricidae; several species of the latter fed on leaf buds). Leaf-miners were common on young leaves (at least four species recorded, mostly Gracillariidae). Cicadellidae and Aphididae were species-rich or abundant. Herbivore densities were generally low but were much higher on young than on mature leaves, the latter being quite tough. Scavengers were mostly represented by Blattidae, Entomobryidae, and presumably some species of Staphylinidae. The small and dense flowers of this tree were attractive to a number of beetles, such as Anthicidae and Cantharidae, and were also visited by predators such as Mantidae. Formicidae were often abundant, and some species nest on the foliage.

Piper. Chewing species were mostly represented by a few species of Chrysomelidae (Alticinae), Geometridae, and Curculionidae. The proportion of specialist species was rather low. Sap-suckers were prominent and were dominated by Cicadellidae, Derbidae, Lygaeidae, Aphididae, and Cercopidae. Some predators, such as Coccinellidae, Anthocoridae, and Hemerobiidae, may have been feeding on aphids and other sap-suckers. Some Cicadellidae and Cercopidae appeared to be xylem-feeders, sometimes rejecting copious amounts of sap on the foliage. This may enhance growth of molds and fungi, on which several fungal-feeding beetles may have been feeding (e.g., Biphyllidae, Lathridiidae, and Mycetophagidae). Although some Formicidae established their nests on the foliage, none were found inside the stems of the host.

Ficus. Densities of both sap-sucking and chewing species were relatively high, with a high proportion of specialists for the latter. Chewers were dominated by Chrysomelidae, Lymantriidae, Tortricidae, Crambidae, and Cerambycidae, whose larvae can presumably develop easily in the hollow twigs of the upper crown. Sap-suckers were dominated by Cicadellidae, Derbidae, Pentatomidae, Lygaeidae, Ricaniidae, and Flatidae. Coccinellidae were relatively abundant on the foliage. The soft wood offered a good habitat for some scavengers (Blattellidae, Tenebrionidae) and wood-borers (Cerambycidae, Buprestidae). Formicidae were common, although they did not establish their nests on the foliage, but, presumably, in dead branches.

Pipturus. Most chewing insects were represented by Chrysomelidae (Eumolpinae), Noctuidae, Choreutidae, Nymphalidae, and Tettigoniidae, which attained high densities. The proportion of specialists was rather high. Sap-suckers were also abundant, including mainly Lygaeidae, Cicadellidae, Plataspidae, and Membracidae. Cecidomyiidae, Miridae, Corylophidae, and Coccinellidae also foraged commonly on the foliage. Formicidae, despite being relatively abundant, were not observed nesting on the foliage.

Castanopsis. This tree was colonized by a species-rich, specialized fauna of leaf-chewers, mostly represented by Lepidoptera: Noctuidae, Geometridae, Tortricidae, Lymantriidae, and Drepanidae. Leaf-miners were common (mainly Gracillariidae). Cicadellidae, Aphididae, Lygaeidae, and Plataspidae were species-rich or abundant among sap-suckers, but these attained lower densities than leaf-chewers and were mostly restricted to young foliage. Predators and parasitoids well represented included Coccinellidae, Staphylinidae, Hemerobiidae, Mantispidae, Braconidae, and Pteromalidae. Cecidomyiidae and Stratiomyidae were also common. Formicidae were abundant and often established their nests in the foliage.

Caldcluvia. Overall, the proportion of specialized leaf-chewers was not high on this tree. These were dominated by Curculionidae, Chrysomelidae, Tortricidae, and Phasmatidae. A tortricid was also a common stem-borer. Psyllidae, Cicadellidae, and Cixiidae were well represented; the former included one unidentified species that formed characteristic leaf galls and attained high densities. Among nonherbivores, Platypodi-

dae, Biphyllidae, Brentidae, Pselaphidae, and Enicocephalidae were relatively common.

Aleurites. Both the densities of herbivores and the proportion of leaf-chewing specialists were low on this tree. The latter were dominated by Limacodidae, Lymantriidae, and Chrysomelidae, and prominent sap-sucking families included Cicadellidae, Lygaeidae, Coccoidea, Tropiduchidae, Ricaniidae, and Derbidae. Common nonherbivores included Anthicidae, Anthribidae, Cerambycidae, Coccinellidae, and Encyrtidae.

Melicope. Chewers, often not highly specialized, were dominated by Geometridae, Curculionidae, Papilionidae, Chrysomelidae, Lecithoceridae, and Tortricidae. Leaf-miners were common (Gracillariidae). Most sap-suckers were Cicadellidae, Aphididae, Lygaeidae, Derbidae, and Fulgoridae. Herbivore densities were rather low. Corylophidae, Anthocoridae, Miridae, and Phlaeothripidae were also abundant on this tree. Formicidae sometimes established nests on the foliage.

Cordia. Herbivore densities were high on this tree. Leaf-chewers were dominated by Lepidoptera: Noctuidae, Geometridae, and Tortricidae. Skeletonizers (some Choreutidae) were common. Tingidae, Cicadellidae, Flatidae, and Pentatomidae dominated sap-suckers. Among nonherbivores, Miridae, Eulophidae, Hemerobiidae, and Formicidae were common on the foliage.

Similarities between the Study Trees: Specialist Leaf-Chewers

When the analyses were performed with the number of individuals, the environmental variables that we chose for the CCA explained 71% of the variance within the system (Table 2). Correlations of the scores for families between the CCA and the CA were good (Table 2), suggesting that the constraints that we imposed on the system did not greatly distort the actual observations. The plane formed by canonical axes 1 and 2 explained 60% of the variance explained by the CCA (Table 2). However, the formation

TABLE 2

SUMMARY STATISTICS FOR THE DIFFERENT CCA PERFORMED

				Correlation CCA-CA[d]					Best explaining variable[f]			
ANALYSIS	EgCCA[a]	EgCA[b]	%[c]	A1	A2	A3	A4	Var 1,2[e]	A1	A2	A3	A4
Specialists—individuals	1.592	2.241	71.0	0.96	0.83	0.92	0.87	59.9	Sus	Yol	Tax	Pal
									0.87	−0.52	−0.61	0.62
Specialists—species	1.134	1.603	70.7	0.96	0.91	0.96	0.97	55.8	Sus	Yol	Tax	Pal
									0.82	0.57	−0.64	0.76
Leaf-chewers—individuals	1.097	1.761	66.8	0.98	0.96	0.98	0.95	60.9	Yol	Pal	Slw	Sus
									−0.62	0.91	−0.77	0.17
Leaf-chewers—species	0.798	1.157	44.0	0.97	0.98	0.96	0.90	54.9	Sus	Yol	Pal	Slw
									0.71	−0.56	−0.82	−0.92
Herbivores—individuals	1.234	1.703	72.5	0.99	0.90	0.94	0.93	63.4	Slw	Yol	Lar	Sus
									−0.62	0.57	−0.87	−0.88
Herbivores—species	0.308	0.423	72.8	0.97	0.99	0.93	0.95	56.5	Yol	Lar	Slw	Sus
									0.60	0.56	−0.89	−0.76
All insects—individuals	0.627	0.840	74.6	0.95	0.97	0.99	0.94	56.2	Slw	Sus	Hei	Bak
									0.69	0.43	−0.76	−0.84

[a] Sum of the eigenvalues for the CCA (EGCCA).
[b] Sum of the eigenvalues for the corresponding CA (EGCA).
[c] Percentage of variance explained by the environmental variables (100 × EG1/EG2).
[d] Correlations of the species score on the first four axes between the CCA and the CA.
[e] Percentage of variance accounted for by the plane formed by axes 1 and 2 (Var 1,2) in the CCA.
[f] Best explaining variables for the formation of canonical axes 1–4, with their canonical correlations. Codes of variables: Bak, bark type; Hei, height; Lar, leaf area; Pal, leaf palatability; Slw, specific leaf weight; Sus, successional status; Tax, taxonomic isolation; Yol, sum of young leaves recorded.

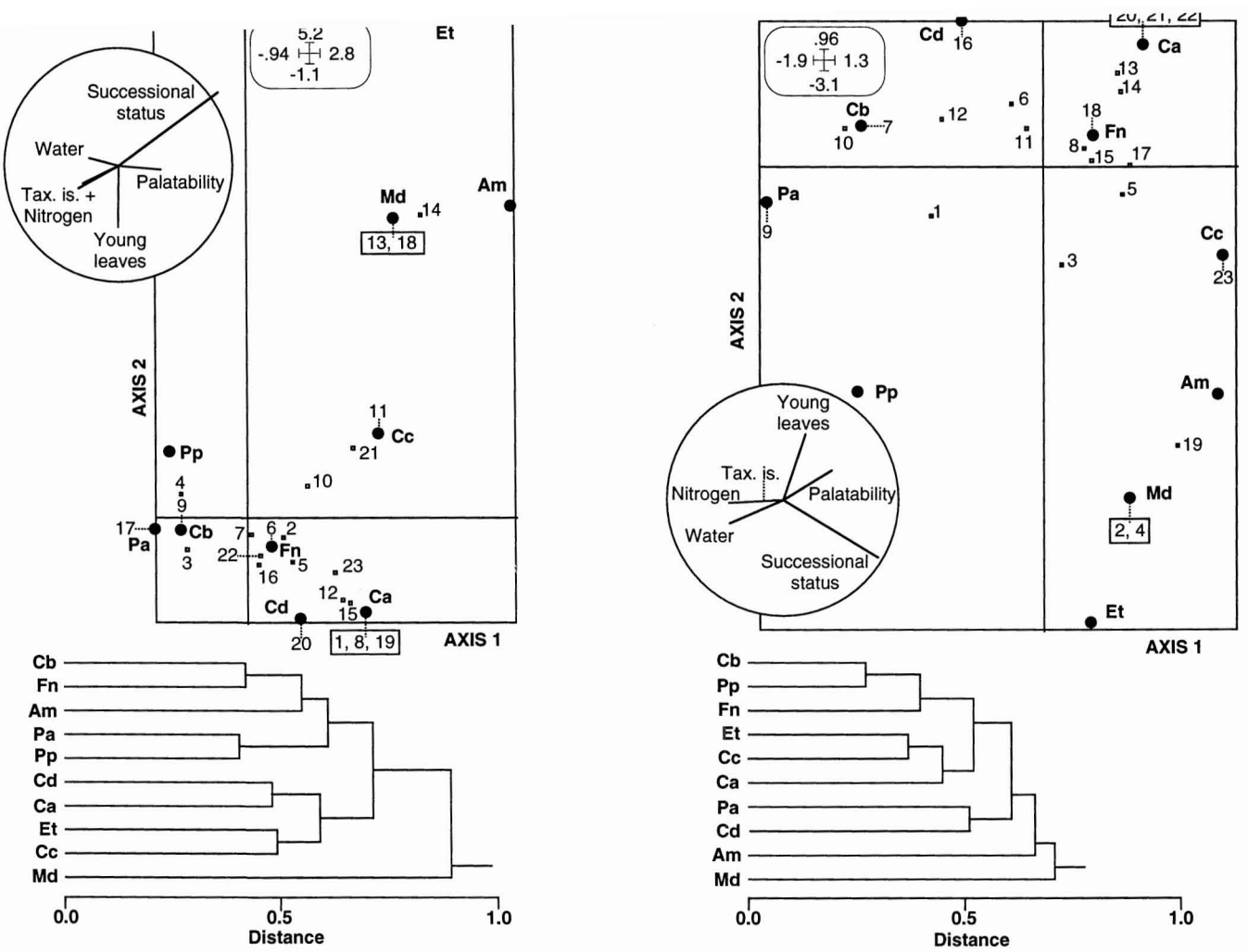

FIGURE 1. CCA diagram (above, plot of canonical axes 1 and 2) and UPGMA clustering (below) for the most common families of specialist leaf-chewers, based on the number of individuals (*a*) and on the number of species (*b*) collected per insect family. Tree species are identified by their initials (see Table 1); insect families are coded as follows: 1, Attelabidae; 2, Cerambycidae; 3, Choreutidae; 4, Chrysomelidae; 5, Crambidae; 6, Arctiidae (Ctenuchinae); 7, Curculionidae; 8, Drepanidae; 9, Gelechiidae; 10, Geometridae; 11, Gracillariidae; 12, Immidae; 13, Lecithoceridae; 14, Limacodidae; 15, Lymantriidae; 16, Noctuidae; 17, Nymphalidae; 18, Papilionidae; 19, Psychidae; 20, Pterophoridae; 21, Pyraloidea; 22, Tettigoniidae; 23, Tortricidae. In the CCA diagram, environmental variables are plotted in a correlation circle with a radius of 1 (not drawn to the same scale).

of the canonical axes was difficult to infer from the environmental variables (Figure 1*a*, Table 2). Axis 1 was best correlated with successional status, thus creating a sun–shade gradient (left and right part of the ordination, respectively). Axis 2 was best correlated with the estimate of the number of young leaves recorded year-long. However, the weakness of the relationships suggests, particularly for axis 2, that the axes may be correlated to other, nonmeasured, variables, perhaps related to some aspects of leaf biochemistry and/or of tree phenology. The UPGMA (Figure 1*a*) further grouped *Caldcluvia*, *Pipturus*, *Piper*, *Ficus*, and *Aleurites* together and *Cordia*, *Castanopsis*, *Elmerrillia*, and *Cinnamomum* into a second group. The first group of trees supported many Coleoptera, whereas the second was more dominated by Lepidoptera.

The analyses performed with the number of species within each family (Table 2, Figure 1*b*) yielded similar results, and our interpretation of the canonical axes was neither changed nor improved. However, the UPGMA (Figure 1*b*) did not show two obvious groups as previously (and this is also reflected by the more spread scores of the trees in the plane formed by canonical axes 1 and 2). At the most, two groups could be distinguished: *Caldcluvia*, *Piper,* and *Ficus* in one and *Elmerrillia*, *Cinnamomum,* and *Castanopsis* in the other. As previously, the groups reflected the dominance of either Coleoptera or Lepidoptera, respectively. The groups of trees were overall more similar when species numbers were used instead of individual numbers (compare the distances of both UPGMA).

Similarities between the Study Trees: Leaf-Chewers

When individuals were considered for this analysis, the environmental variables explained 67% of the total variance in the system (Table 2). The first axis was best related with the number of young leaves recorded, whereas the second axis was more clearly related to leaf palatability. The interpretation of the third axis was also possible, with leaf weight scoring highly on this axis. The cluster analysis clearly segregated two groups: *Caldcluvia*, *Pipturus*, *Piper*, *Ficus*, *Melicope* (and to a lesser extent *Aleurites*) and *Cordia*, *Castanopsis*, *Cinnamomum,* and *Elmerrillia* (Figure 2*a*). These groups were slightly different than in the previous analyses, with *Melicope* joining the rest of the trees much sooner than previously. The sun–shade and the Coleoptera–Lepidoptera gradients observed for the specialist leaf-chewers were no more apparent. Causative factors for tree similarity were not as apparent as previously, but may be marginally related to leaf palatability and leaf weight.

The analyses performed with the number of species appeared less robust and, in particular, the environmental variables explained less of the total variance in the system (44%; Table 2). Among these, successional status, leaf palatability, and leaf weight appeared important. The trees were more similar in these analyses, and the only clear distinction that could be distinguished was a group of *Caldcluvia*, *Piper*, and *Ficus* and another of *Cordia*, *Cinnamomum,* and *Castanospsis* (Figure 2*b*).

Similarities between the Study Trees: Herbivores

The environmental variables accounted for about 73% of the total variance when the system was described by the number of individuals (Table 2). However, the first two canonical axes were difficult to interpret in light of the variables measured. Axes 3 and 4 were best related to leaf area and successional status, respectively. Two groups were distinguishable: *Caldcluvia*, *Pipturus*, and *Melicope* and *Piper*, *Ficus*, *Castanopsis*, and *Cinnamomum*. The rest of the trees joined these groups at greater distances (Figure 3*a*). It was difficult to interpret these groups in light of the variables measured.

The CCA performed with the number of species was equally difficult to interpret. Again, about 73% of the variance was explained by the environmental variables, and leaf weight and successional status scored highly on axes 3 and 4, respectively. Trees appeared much more similar when using

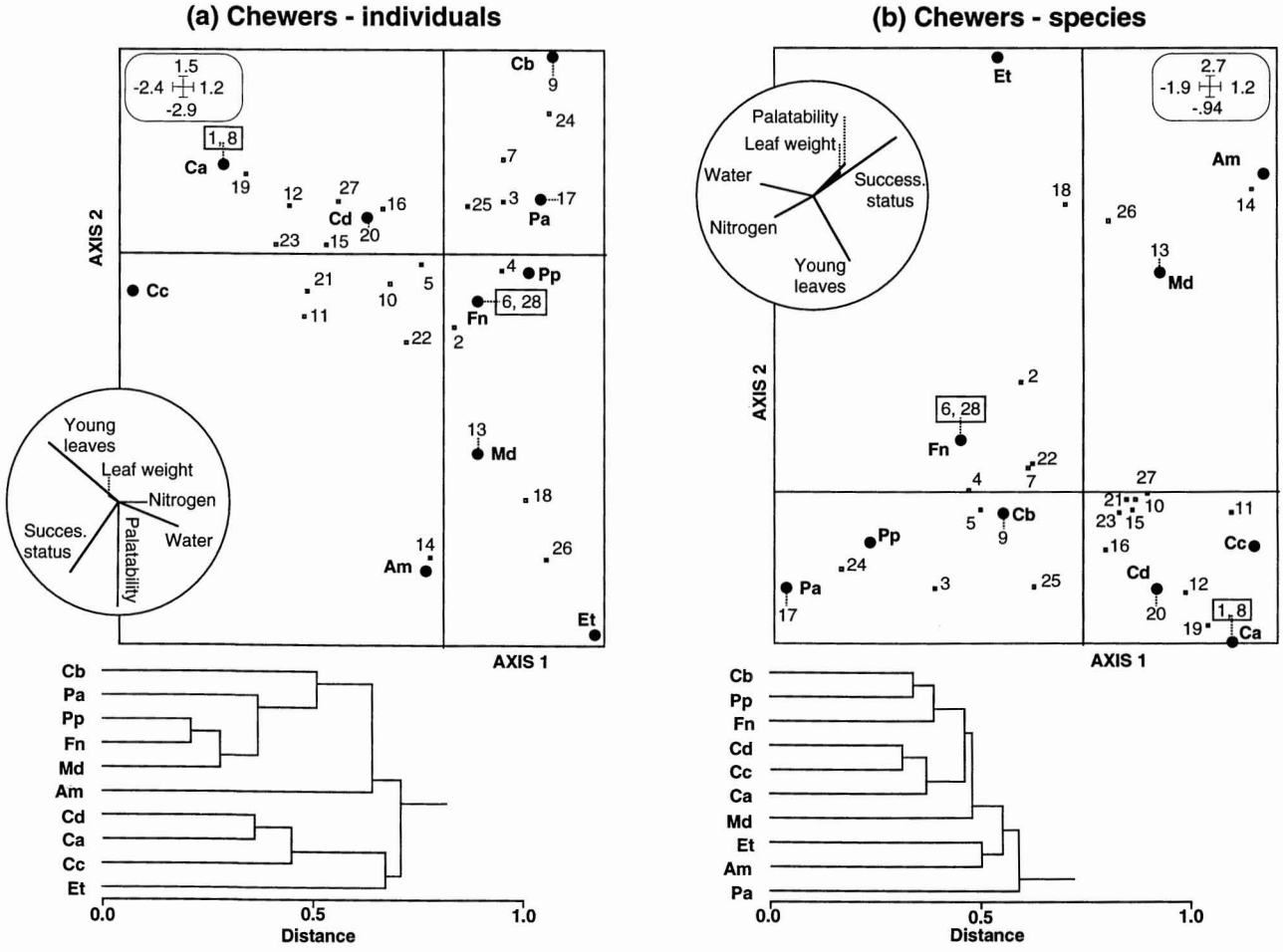

FIGURE 2. CCA diagram (above, plot of canonical axes 1 and 2) and UPGMA clustering (below) for the most common families of proven leaf-chewers, based on the number of individuals (*a*) and on the number of species (*b*) collected per family. Presentation follows that of Figure 1. Additional families, not included in Figure 1, are as follows: 24, Acrididae; 25, Arctiidae; 26, Lagriidae; 27, Phasmatidae; 28, Tineidae.

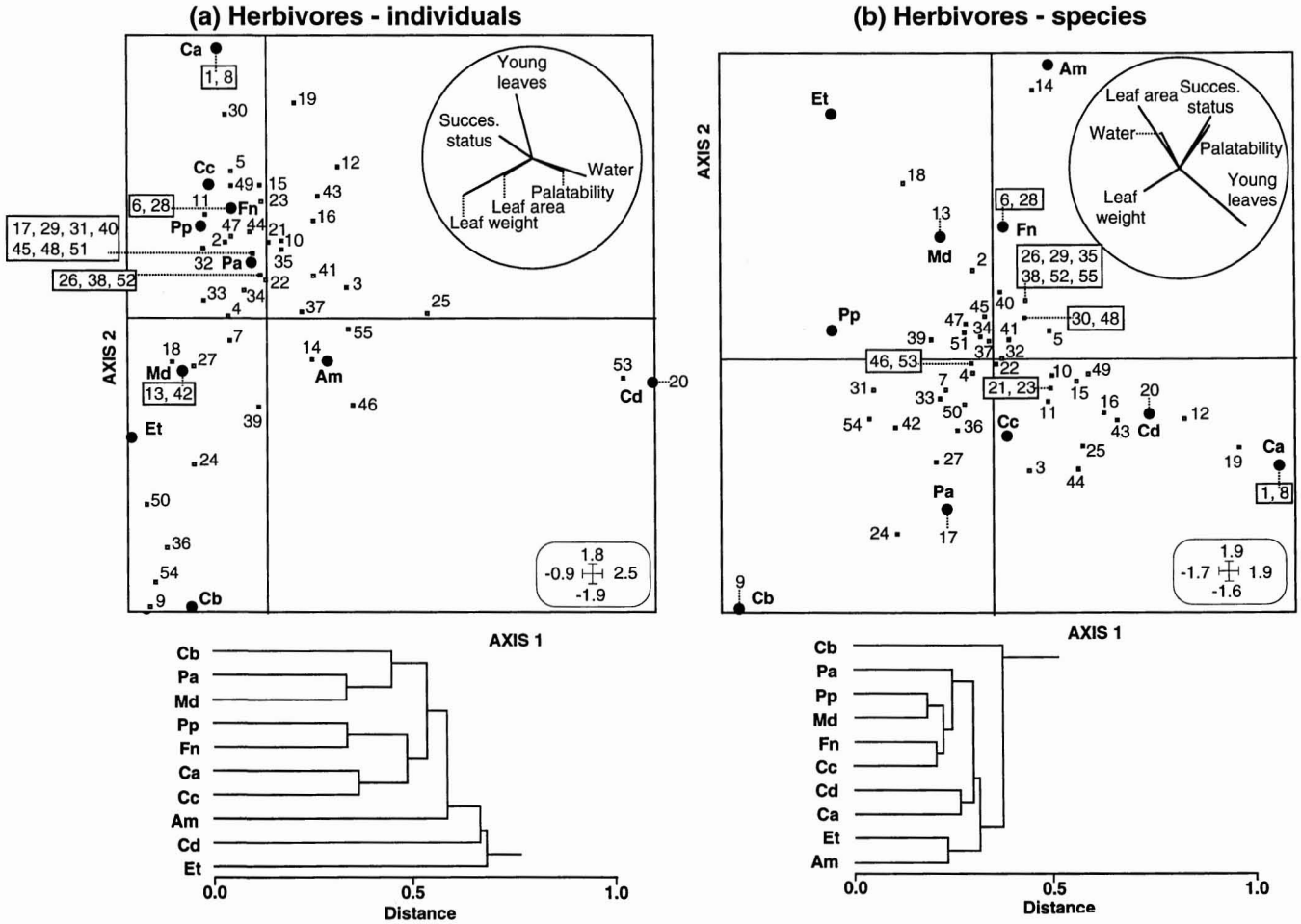

FIGURE 3. CCA diagram (above, plot of canonical axes 1 and 2) and UPGMA clustering (below) for the most common families of herbivores, as based on the number of individuals (*a*) and on the number of species (*b*) collected per family. Presentation follows that of Figure 2. Additional families, not included in Figure 2, are coded as in Appendix 2.

number of species than when using number of individuals. The clustering of the trees was much different than previously, with little congruence (Figure 3*b*).

Similarities between the Study Trees: All Insects

The environmental variables explained nearly 75% of the total variance in this analysis. However, only tree height (for axis 3) and bark type (for axis 4) clearly appeared to be of some importance in the formation of the canonical axes. Three groups were apparent in the UPGMA: *Pipturus* and *Melicope*; *Piper*, *Cinnamomum*, and *Castanopsis*; and *Ficus*, *Elmerrillia*, and *Aleurites*. *Cordia* and, notably, *Caldcluvia* joined the rest of the trees at greater distances (Figure 4). The primary reasons for such groupings (i.e., the first canonical axes) were difficult to infer, but secondary reasons appeared to be related to tree architecture (e.g., height, type of bark, leaf weight), as indicated by the canonical correlations (Table 2).

Host-Tree Phylogeny

The higher classification of flowering plants remains quite unstable, but for the purpose of comparisons of herbivore faunas, the relationships of the 10 host trees were approximated by the dendrogram in Figure 5. The dendrogram is based largely on the hierarchical classification of Cronquist (1988), modified with reference to Chase et al. (1993, especially figs. 2 and 11*A*, with respect to the polyphyletic Hamamelidae). It is obvious that none of the seven clusters generated by insect data (Figures 1–4) approaches this dendrogram, and, at our level of analysis, we must conclude that host phylogeny does not strongly influence faunal similarity among hosts.

DISCUSSION

Measuring Faunal Similarities of Tropical Trees

Our analyses of tree similarity with insect families were performed with data obtained from local insect faunas. We do not know whether our findings could apply to regional insect faunas (i.e., insect faunas supported over most of the area of geographic distribution of the host tree). When the association of insects with the tree species from which they had been collected was ascertained, the clustering of tree species was more or less similar when expressed either by the number of individuals or the number of species within insect families (e.g., analyses for specialist leaf-chewers and proven leaf-chewers). When this association was not ascertained (e.g., analysis for all herbivores), the results were quite different using either the number of individuals or the number of species. Using the number of species resulted systematically in increased similarities among the tree species, compared with using the number of individuals (compare the distances in each pair of clusters in Figures 1–3). Further, in most cases, the CCA performed with the number of individuals appeared more robust that that performed with the number of species (compare the percentage of total variance explained by the different CCAs in Table 2).

Thus, our data suggest, for the type of analyses of similarity undertaken, that it may be more meaningful to fill the data matrices with the number of individuals rather than with the number of species, particularly in cases where the association between the putative host and the insects collected on its foliage has not been ascertained. In those cases, the prevalence of transient species (i.e., herbivore species resting on the foliage but not feeding on it) on the foliage of tropical trees (Basset in press) certainly limits the meaningfulness of analyses performed with the number of species. Transient species may obscure interesting patterns of community structure and/or faunal similarity. This is much less likely to occur when the number of individuals is considered, because transient herbivore species typically occur in low numbers in samples of tropical vegetation (Basset in press). Stork (1987*a*) reported that the distance between trees that were fogged in a Bornean lowland rain forest was an important determinant of faunal similarity for Homoptera, but was unable to explain this observation. It is possible that this resulted from

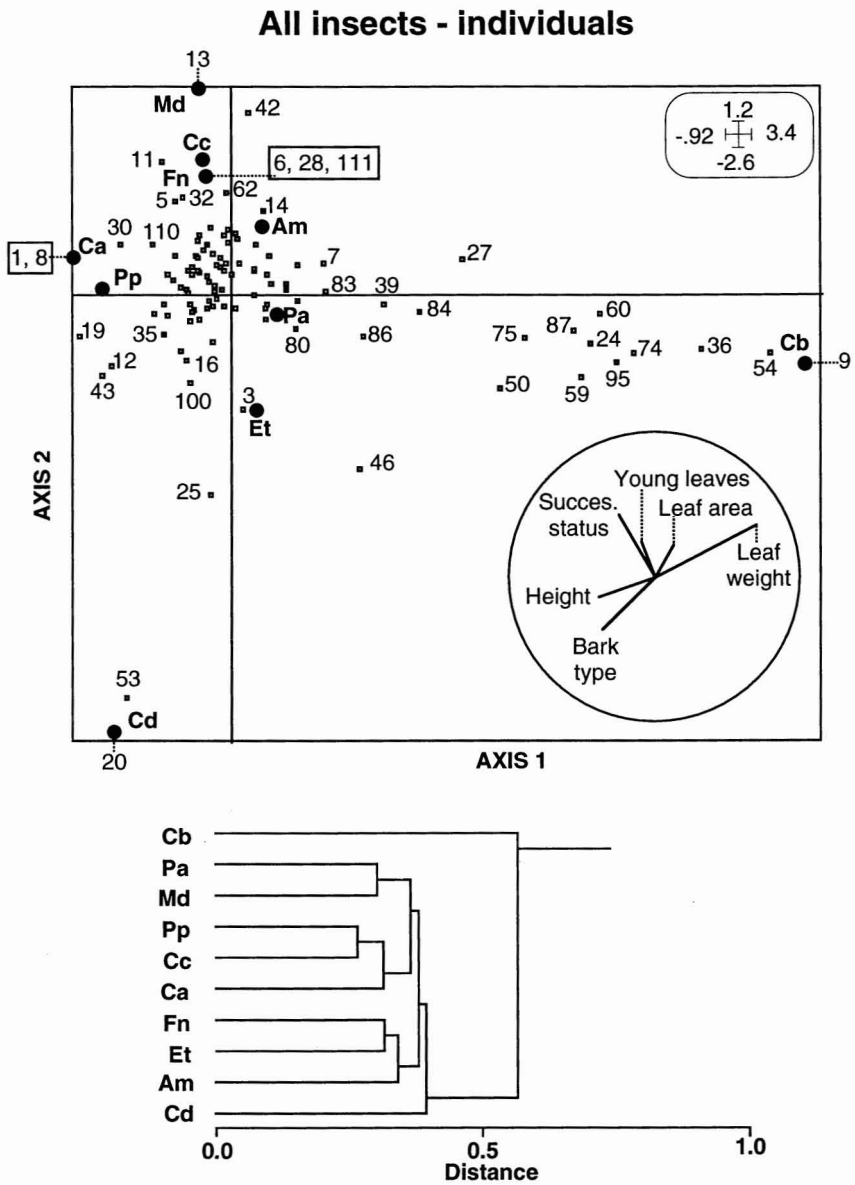

FIGURE 4. CCA diagram (above, plot of canonical axes 1 and 2) and UPGMA clustering (below) for the most common insect families, as based on the number of individuals collected per family. Presentation follows that of Figure 3. Additional families, not included in Figure 3, are coded as in Appendix 3. For the sake of clarity, code numbers of insect families in the center of the plot are omitted.

including transient species in the analysis (the closeness of association between herbivores and their hosts was not ascertained in Stork's study), because close trees in a forest may experience similar influxes of transient species coming from similar surrounding vegetation.

Stork (1987*b*) further observed that there was considerably more variation in the relative proportion of chewing to sap-sucking

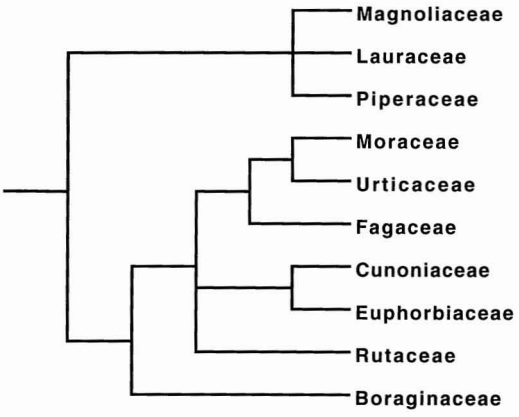

FIGURE 5. Dendrogram representing host-tree phylogeny (see text). Hosts are designated by their families.

insects when the number of individuals was considered than when the number of species was considered. He recognized the problem of transient species for herbivorous species and further suggested that the constancy of proportion for some arthropod guilds (Moran and Southwood 1982, Stork 1987*b*) may be theoretical and not a biological reality, and that, in this case, the number of individuals or biomass may be more meaningful reflections of guild structure. Our data tend to support his views for tropical trees, particularly when the associations between the putative hosts and the insects have not been ascertained. For temperate trees, the situation may be different. Cornell and Kahn (1989) analyzed the guild structure of insects associated with British trees and concluded that there was a moderately strong correlation between the number of species in the chewing and sap-sucking guilds. Similar analyses for tropical trees need the closeness of insects with their putative hosts to be reported for both leaf-chewers and sap-suckers.

Finally, our data showed clearly (compare the last joining distance in clusters for the number of individuals in Figures 1–4) that faunal similarity became increasingly similar along the following sequence: specialist leaf-chewers–leaf-chewers–herbivores–all insects. This is not unexpected because many non-herbivore groups are not particularly specialized with regard to the choice of a tree species (e.g., Basset 1992). They may be more specialized in terms of microhabitat choices within the arboreal habitat. Thus, levels of faunal similarity clearly depend on the insect groups targeted and their feeding habits, as shown by Stork (1987*a*) with different aims and methods.

Why Are Tropical Trees Sometimes Similar in Terms of Insect Families?

The putative reasons for tropical trees showing convergence or divergence in faunal similarity are certainly complex. Most likely, causative factors are many, as suggested by the spread of the total variance explained by the CCAs over different canonical axes. Most of these axes were difficult to interpret, suggesting that the system was influenced by other variables that had not been measured. Among these may be biogeographical and historical factors; tree abundance; epiphytic load; denseness, apparency, and reflectance of foliage; synchronicity of host phenology; surrounding vegetation; litter and soil characteristics; microclimate, etc. Some of these variables may differ significantly only between individual trees of the same species; others may vary significantly both within individuals and within species of trees.

Our data nevertheless suggest that for specialist leaf-chewers, the successional status of the host is an important factor that, to some extent, could explain convergence in faunal similarity of either pioneer or persistent tree species. In our system, the fauna of pioneer trees was often dominated by some beetle families, whereas that of persistent trees was more likely to be dominated by lepidopteran families. The distribution of particular beetle and lepidopteran families in pioneer and persistent trees is unlikely to be similar at different locations and may only reflect the local characteristics of the system studied (for different results, see, e.g., Greenwood [1990]; for a general discussion about the distribution of moth families in disturbed habitats, see, e.g., Holloway et al. [1992]). However, the general habitat in which the tree species grows (e.g., edges, clearings, or deep forest)

could explain convergences in faunal similarity (Futuyma and Gould 1979). Other faunal similarities and contrasts may arise from subtle differences and similarities in the biochemistry of the host, its past history, and in the microhabitats that it provides to its associated fauna.

For leaf-chewers in general, the primary reason for faunal differences/similarities among the study trees was difficult to determine. Consequently, it was also difficult to interpret the clustering of tree species, as it was in analyses including all herbivores and all insects. Secondary factors of some importance in the analysis performed with leaf-chewers included leaf palatability and leaf weight. These gross features of the hosts may be of particular importance to generalist species. When all herbivores were included in the analyses, the interpretation of causal factors was even more difficult, but could be related, marginally, to leaf area (perhaps itself related to foliage denseness) and to successional status. In this case, it is probable that host features affecting flight and alighting of insect herbivores, such as foliage reflectance (Prokopy and Owen 1983), may be important.

Eventually, when all insect families were considered, although study trees appeared more similar overall than in previous analyses, the primary factors for this convergence were again difficult to interpret. However, secondary factors were clearly related to host architecture: tree height and type of bark. Both variables may be related to the number of microhabitats, feeding sites, and sheltering sites available (Lawton 1983).

Stork (1987*a*), fogging rain forest trees in Borneo, found that taxonomic relatedness of the study trees was an important determinant of faunal similarity for certain insect groups only but that the variance explained by this variable was low (despite the fact that one level of scoring for taxonomic similarity was "same species," because some individual trees of the same species were fogged). Our data suggest that transient species may artificially increase the similarity of study trees, so it is possible that Stork's results for herbivore species may have been influenced by transient species. When we considered specialist leaf-feeders, the effect of taxonomic isolation of the tree was not evident and there was little congruence between tree phylogeny and faunal similarity. Thus, taxonomic similarity of trees appears not to influence strongly the faunal similarity of tropical trees, but this effect may become apparent only when specific insect groups are examined at a high taxonomic resolution (e.g., Holloway and Hebert 1979, Perrin 1992).

CONCLUSIONS

To conclude with the implications of our findings for the biological conservation of tropical arboreal arthropods, we can ask the following questions, with particular regard to our system: what would be the outcome for the insect fauna of particular tree species being removed from the system? Would this effect be different if different tree species are removed? Could certain tree species be considered "keystone species" in the sense that their removal will result in numerous insect extinctions (see Mills et al. 1993)? For the first question, our data suggest that, not unexpectedly, specialist herbivores associated with the extinct tree species will also disappear and along with them associated specialist predators and parasitoids. Generalist herbivores could still thrive, particularly if there remains in the system a few tree species of high palatability and low leaf weight. Some nonherbivore species, particularly fungal-feeders, wood-borers, and scavengers, may probably also subsist, providing that a few tree species of complex architecture (e.g., tall, with complex bark), providing a variety of microhabitats and feeding sites, also subsist.

It is also evident that the magnitude of loss in insect species following the loss of their host will depend on the characteristics of that tree species and whether it supports a distinct insect fauna. Our brief descriptions of the insect faunas associated with the study trees emphasized that none of the host trees are identical in that regard. In no case will the removal of a single tree species result in

the disappearance of half of the insect species. Rather, our data suggest that nearly three-fourths of the species of leaf-chewers in our system (288 out of 398 species, 72%) may be preserved if half of the most faunistically speciose tree species are preserved (*Castanopsis*, *Ficus*, *Pipturus*, *Cordia,* and *Caldcluvia*). Note that this includes preserving both pioneer and persistent host species. These views are undoubtedly simplistic, because the total disappearance of particular tree species is likely to occur when the system has been deeply altered. The "importance" of insect species in the food chain of tropical forests may also differ from one species to another (e.g., some herbivore species may be attacked by more predators and parasitoids than others). Further, the degree of host specificity and endemism in insect herbivores is likely to vary from one tropical location to another (Y.B., unpubl. data).

To conclude, our understanding of insect-plant interactions in tropical systems, and our abilities to manage them, will certainly depend on our future aptitude in developing efficient and swift techniques to study the ecology of the countless insect species that inhabit tropical trees.

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APPENDIX 1

CHEWING INSECTS FEEDING ON THE STUDY TREES, DETAILED BY TREE SPECIES AND BY FAMILIES

TREE TAXA	INSECT TAXA	STATUS[a]	NO. SP.	NO. INDIVIDUALS
Elmerrillia tsiampacca	Cerambycidae	0/2/1	3	3
	Chrysomelidae	0/2/0	2	5
	Rhyparidella? sp.	ge	—	1
	Rhyparidella? sp.	ge	—	4
	Curculionidae	1/0/0	1	1
	Geometridae	1/0/2	3	8
	Lagriidae	0/0/2	2	32
	Lymantriidae	0/1/0	1	6
	Noctuidae	0/1/0	1	2
	Papilionidae	0/0/3	3	4
	Pyraloidea	1/0/1	2	7
	Tortricidae	0/2/0	2	6
Cinnamomum cf. *culilaban*	Cerambycidae	1/0/0	1	1
	Chrysomelidae	1/0/0	1	2
	Rhyparida sp.	sp	—	2
	Curculionidae	1/1/0	2	5
	Geometridae	5/5/0	10	44
	Anisodes sp.	sp	—	12
	Ectropis bhurmitra Walker	ge	—	3
	Gracillariidae	1/0/2	3	9
	Phyllocnistis sp.	un	—	4
	Immidae	1/0/0	1	1
	Lymantriidae	0/4/0	4	8
	Dascychira plagosa Rothschild	ge	—	1
	Noctuidae	1/2/0	3	4
	Phasmatidae	1/0/1	2	6
	Pyraloidea	1/0/2	3	23
	Tettigoniidae	0/2/0	2	9
	Tortricidae	3/3/3	9	110
	Adoxophyes sp.	un	—	1
	Lopharca sp.	un	—	4
	Sorolopha cyclostoma Lower	ge	—	16
	Sorolopha ?compstitis Meyrick	ge	—	71
	Sorolopha ?melanocycla Diakonoff	sp	—	10
	Sorolopha sp.	sp	—	1
Piper plagiophyllum	Chrysomelidae	4/0/0	4	236
	Aulacophora sp.	sp	—	1
	Crepidodera sp.	sp	—	189
	Stethotes sp.	sp	—	1
	Xenidea sp.	sp	—	45
	Curculionidae	1/3/0	4	17
	Geometridae	1/3/2	6	72
	Milionia sp.	sp	—	27
	Ectropis bhurmitra Walker	ge	—	35
	Noctuidae	0/1/0	1	3
	Tortricidae	0/3/0	3	6
	Isotenes sp.	ge	—	1
Ficus nodosa	Cerambycidae	3/3/1	7	16
	Hestima sp.	ge	—	1
	Rosenbergia vetusta Ritsema	ge	—	1
	Xiphotheota sp.	sp	—	10
	Chrysomelidae	4/7/0	11	294
	Atysa sp.	sp	—	18
	Aulacophora sp.	sp	—	4
	Coenobius kleinhoviae Gressitt	sp	—	4

APPENDIX 1 (continued)

TREE TAXA	INSECT TAXA	STATUS[a]	NO. SP.	NO. INDIVIDUALS
	Rhyparida coriacea Jacoby	ge	—	11
	Rhyparidella wauensis Gressitt	ge	—	53
	Rhyparidella? sp.	ge	—	4
	Rhyparidella? sp.	ge	—	39
	Rhyparidella? sp.	ge	—	46
	Crambidae	2/1/0	3	15
	Glyphodes stolalis Guénée	sp	—	2
	Talanga sp.	sp	—	12
	Arctiidae (Ctenuchinae)	1/0/0	1	5
	Curculionidae	3/1/0	4	44
	Viticis sp.	sp	—	21
	Apirocalus ?ebrius Faust	ge	—	8
	Geometridae	2/2/1	5	54
	Hyposidra talaca Walker	ge	—	1
	Immidae	0/0/1	1	2
	Imma ?itygramma Meyrick	un	—	2
	Lymantriidae	5/3/0	8	19
	Euproctis sp.	sp	—	1
	Noctuidae	3/1/0	4	10
	Tiracola plagiata Walker	ge	—	1
	Nymphalidae	2/0/1	3	4
	Pyraloidea	2/1/0	3	10
	Tettigoniidae	1/0/0	1	4
	Tineidae	0/1/0	1	4
	Tortricidae	5/1/0	6	22
	Undetermined Microlepidoptera	2/1/0	3	4
Pipturus argenteus	Acrididae	3/0/0	3	7
	Arctiidae	0/1/0	1	8
	Cerambycidae	0/0/2	2	2
	Choreutidae	3/0/0	3	41
	Choreutis porphyratma (Meyrick)	sp	—	24
	Chrysomelidae	9/3/2	14	326
	Manobia sp.	sp	—	38
	Neolepta? sp.	sp	—	4
	Neolepta? sp.	un	—	1
	Oides sp.	sp	—	29
	Rhyparida sp.	sp	—	22
	Rhyparidella wauensis Gressitt	ge	—	113
	Rhyparidella? sp.	ge	—	19
	Rhyparidella? sp.	sp	—	10
	Rhyparidella? sp.	sp	—	16
	Rhyparidella? sp.	un	—	2
	Sastra sp.	ge	—	5
	Stethotes integra Baly	sp	—	37
	Stethotes sp. nr *lateralis* Baly	sp	—	21
	Stethotes sp.	sp	—	9
	Crambidae	1/0/0	1	1
	Pleuroptya sp. nr *sabinusalis* (Walker)	sp	—	1
	Curculionidae	1/4/1	6	72
	Apirocalus ?ebrius Faust	ge	—	44
	Gymnopholus weiskei Heller	ge	—	2
	Paepalophorus frontalis Pascoe	sp	—	18
	Geometridae	0/0/1	1	3
	Agathiopsis basipuncta Warren	un	—	3
	Lymantriidae	0/0/1	1	1
	Noctuidae	5/1/2	8	74
	Arcte coerula Guénée	sp	—	26

APPENDIX 1 (continued)

TREE TAXA	INSECT TAXA	STATUS[a]	NO. SP.	NO. INDIVIDUALS
	Dinumma sp. nr *oxygrapha* (Snellen)	un	—	1
	Hypena sp. prob. *hedychroa* Bethune-Baker	sp	—	37
	Hypena sp. prob. *nuta* Swinhoe	sp	—	1
	Nymphalidae	3/0/0	3	66
	Mynes geoffroyi Guérin-Méneville	sp	—	5
	Symbrenthia hippoclus Cramer	sp	—	29
	Tettigoniidae	1/3/2	6	12
	Tortricidae	1/1/1	3	11
	Homona sp.	sp	—	8
Castanopsis acuminatissima	Attelabidae	1/0/0	1	5
	Cerambycidae	0/1/0	1	3
	Chrysomelidae	3/0/1	4	26
	Micromolpus sp.	sp	—	3
	Monolepta? sp.	sp	—	14
	Rhyparidella? sp.	un	—	5
	Thyrasia? sp.	sp	—	4
	Crambidae	1/0/0	1	5
	Agrotera sp.	sp	—	5
	Curculionidae	1/1/1	3	25
	Apirocalus ?ebrius Faust	ge	—	4
	Myllocerus sp.	sp	—	20
	Drepanidae	2/0/1	3	10
	Geometridae	10/5/4	19	41
	Anisodes sp.	un	—	2
	Luxiaria sp.	un	—	1
	Myrioblephara sp. prob. *confusa* Warren	ge	—	4
	Gracillariidae	0/0/1	1	12
	Immidae	2/0/2	4	8
	Lymantriidae	10/1/2	13	59
	Redoa sp.	un	—	4
	Redoa sp.	sp	—	12
	Noctuidae	9/5/4	18	88
	Anigraea sp.	ge	—	25
	Nycteola sp. prob. *brunneicosta* (Bethune-Baker)	un	—	3
	Selepa sp. nr *nigralba* Hampson	ge	—	1
	Oecophoridae?	1/0/0	1	1
	Phasmatidae	1/0/0	1	1
	Psychidae	1/1/0	2	5
	Pyraloidea	2/1/2	5	10
	Tortricidae	7/5/1	13	99
	Dicephalarcha sicca Diakonoff	ge	—	2
	Homona sp.	ge	—	1
	Isotenes sp.	ge	—	6
	Isotenes sp.	sp	—	1
	Undetermined Microlepidoptera	3/0/1	4	5
Caldcluvia brassii	Acrididae	0/1/0	1	10
	Cerambycidae	0/1/0	1	1
	Chrysomelidae	4/0/1	5	148
	Neolepta? sp.	sp	—	6
	Rhyparida sp. (*bryanti* group)	un	—	53
	Rhyparida sp.	sp	—	34
	Rhyparidella? sp.	sp	—	41
	Stethotes suturalis Bryant	sp	—	14
	Curculionidae	1/8/1	10	235
	Apirocalus ?ebrius Faust	ge	—	1
	Gymnopholus interpres Heller	ge	—	10
	Gymnopholus marquardti Heller	ge	—	19

APPENDIX 1 (continued)

TREE TAXA	INSECT TAXA	STATUS[a]	NO. SP.	NO. INDIVIDUALS
	Hellerhinus papuanus (Heller)	ge	—	16
	Oribius sp.	ge	—	2
	Panthorhytes pilosus Heller	ge	—	17
	Elateridae	0/1/0	1	1
	Gelechiidae	1/0/0	1	4
	Geometridae	1/3/0	4	5
	Lymantriidae	0/5/0	5	8
	Noctuidae	2/0/0	2	9
	Phasmatidae	0/3/0	3	6
	Pyraloidea	0/1/1	2	3
	Tortricidae	2/2/0	4	17
Aleurites moluccana	Cerambycidae	0/2/0	2	2
	Chrysomelidae	1/2/0	3	35
	Rhyparidella? sp.	ge	—	29
	Rhyparidella? sp.	ge	—	4
	Rhyparidella? sp.	sp	—	2
	Curculionidae	0/1/0	1	4
	Apirocalus ?ebrius Faust	ge	—	4
	Lagriidae	0/0/1	1	2
	Geometridae	0/2/0	2	9
	Hyposidra talaca Walker	ge	—	8
	Iulotrichia semiumbrata Warren	ge	—	1
	Limacodidae	1/2/3	6	35
	Doratifera rufa Bethune-Baker	un	—	20
	Lymantriidae	0/2/2	4	8
	Euproctis sp.	ge	—	1
	Noctuidae	1/1/0	2	8
	Phasmatidae	0/1/0	1	1
	Tettigoniidae	0/2/0	2	8
	Tortricidae	0/1/0	1	4
Melicope denhamii	Chrysomelidae	0/1/0	1	204
	Rhyparidella? sp.	ge	—	204
	Cosmopterigidae	1/0/0	1	1
	Limnaecia metacypha Meyrick or near	sp	—	1
	Curculionidae	3/5/0	8	29
	Apirocalus ?ebrius Faust	ge	—	1
	Gymnopholus marquardti Heller	ge	—	1
	Gymnopholus urticivorax Gressitt	ge	—	1
	Gymnopholus weiskei Heller	ge	—	9
	Poropterus sp.	sp	—	1
	Geometridae	3/6/0	9	19
	Gracillariidae	0/0/1	1	15
	Acrocercops sp.	un	—	15
	Lecithoceridae	1/0/0	1	31
	Limacodidae	1/0/0	1	4
	Noctuidae	0/2/0	2	2
	Papilionidae	2/0/1	3	4
	Saturniidae	0/0/1	1	1
	Tettigoniidae	3/0/0	3	7
	Tortricidae	2/3/0	5	11
	Undetermined Microlepidoptera	0/0/1	1	1
Cordia dichotoma	Arctiidae	0/2/0	2	6
	Choreutidae	2/0/0	2	12
	Brenthia sp.	sp	—	10
	Chrysomelidae	0/2/0	2	36
	Rhyparidella? sp.	ge	—	12
	Rhyparidella? sp.	ge	—	24

APPENDIX 1 (continued)

TREE TAXA	INSECT TAXA	STATUS[a]	NO. SP.	NO. INDIVIDUALS
	Curculionidae	1/1/0	2	32
	Apirocalus ?ebrius Faust	ge	—	31
	Geometridae	1/4/2	7	46
	Immidae	1/0/0	1	4
	Imma sp.	sp	—	4
	Lagriidae	1/0/0	1	8
	Lymantriidae	1/4/0	5	9
	Euproctis sp.	ge	—	1
	Noctuidae	6/2/1	9	46
	Callyna monoleuca Walker	sp	—	6
	Psychidae	0/1/0	1	1
	Pterophoridae	1/0/0	1	3
	Pyraloidea	2/0/0	2	9
	Tettigoniidae	1/1/0	2	2
	Tortricidae	2/5/0	7	35
	Homona mermerodes Meyrick	sp	—	2
	Homona sp.	ge	—	2
	Homona? sp.	ge	—	2
	Undetermined Microlepidoptera	0/1/0	1	1

NOTE: For sake of brevity, unidentified taxa are pooled by families. In that case, the number of species is detailed under the status column. Data were pooled for all sampling methods used.

[a] sp/ge/un. ge, generalist; sp, specialist; un, unknown.

APPENDIX 2

NUMBER OF MORPHOSPECIES AND INDIVIDUALS OF THE MOST COMMON ADULT CHEWERS (INCIDENTAL AND ADDITIONAL SPECIES, NOT ACCOUNTED FOR IN APPENDIX 1) AND SAP-SUCKERS COLLECTED ON EACH TREE SPECIES

CODE NO.[a]	INSECT TAXA	Et	Cc	Pp	Fn	Pa	Ca	Cb	Am	Md	Cd	TOTAL (ind.)
4.	Chrysomelidae	12/24[b]	27/127	17/50	17/32	18/65	22/112	34/221	12/19	27/148	10/55	853
7.	Curculionidae	14/28	40/120	35/76	32/80	27/530	24/50	59/127	18/57	27/466	21/55	1,589
26.	Lagriidae	1/3	4/11	2/14	5/50	2/10	5/20	—	5/10	5/12	3/13	143
29.	Scarabaeidae	4/9	5/27	4/5	6/74	3/10	4/13	1/16	5/7	3/3	5/7	171
30.	Achilidae	—	1/2	1/1	1/1	1/5	1/30	—	1/1	1/3	—	43
31.	Aleyrodidae	—	—	2/4	—	1/12	—	—	—	—	—	16
32.	Aphididae	1/69	2/231	2/82	2/8	2/3	3/157	2/10	2/4	2/281	2/11	856
—	Aphrophoridae	1/1	1/1	2/2	1/3	—	—	—	—	—	—	7
33.	Cercopidae	1/2	1/1	2/4	1/3	1/1	2/2	3/3	1/1	—	—	17
34.	Cicadellidae	13/38	13/25	18/76	21/119	16/90	19/262	13/151	12/98	23/203	10/77	1,139
35.	Cicadidae	3/23	2/14	3/47	4/25	3/22	4/38	—	3/13	1/6	4/33	221
36.	Cixiidae	1/3	2/2	—	—	1/6	2/2	4/80	1/1	1/3	1/1	98
37.	Coccoidea	1/2	1/2	3/9	2/17	4/13	2/26	2/19	4/61	2/3	3/20	172
38.	Coreidae	1/2	3/3	—	2/10	1/2	2/2	1/1	4/4	2/4	2/2	30
39.	Delphacidae	1/1	1/1	—	1/1	—	—	2/3	1/3	1/1	1/1	11
40.	Derbidae	7/13	6/11	8/19	10/118	4/13	7/8	—	7/18	7/12	5/13	226
41.	Flatidae	2/11	3/11	2/11	5/76	2/5	3/10	1/1	1/31	2/6	3/36	198
42.	Fulgoridae	—	1/1	—	—	—	—	1/1	—	1/12	—	14
43.	Issidae	—	1/1	1/6	—	—	2/6	—	—	—	2/4	17
44.	Largidae	—	1/1	—	—	1/9	1/1	—	—	—	—	11
45.	Lygaeidae	7/40	3/20	5/14	7/34	5/172	8/121	5/13	7/68	7/81	3/8	571
46.	Meenoplidae	1/2	1/3	2/12	2/3	1/3	1/7	2/36	1/1	1/1	3/39	107
47.	Membracidae	3/7	1/1	2/3	1/10	2/24	2/13	1/1	1/1	2/2	1/1	63
48.	Pentatomidae	6/14	5/14	4/14	7/76	3/25	7/28	2/10	3/17	4/9	7/14	221
49.	Plataspidae	1/14	1/9	—	1/18	1/26	3/53	—	—	1/5	2/4	129
50.	Psyllidae	2/555	2/39	4/2,462	2/126	3/72	3/33	4/476	1/334	3/59	4/46	4,202
	Heteropsylla cubana Crawford	17	36	2,457	124	63	25	1	334	57	34	3,148
51.	Pyrrhocoridae	1/3	1/16	2/51	1/61	1/59	1/1	1/1	1/1	2/12	1/13	218
52.	Ricaniidae	4/41	2/5	3/5	4/104	3/13	4/12	—	3/50	2/4	3/12	246
—	Scutellaridae	—	—	—	—	1/1	2/3	—	1/1	—	1/1	6
—	Tessaratomidae	1/1	—	—	—	1/1	—	—	—	1/4	—	6
53.	Tingidae	3/5	2/4	1/13	3/14	3/3	2/3	3/6	1/6	2/18	3/950	1,022
54.	Triozidae	—	—	—	1/2	—	—	1/30	—	—	—	32
55.	Tropiduchidae	1/4	1/3	1/8	1/12	1/1	1/5	—	1/91	1/1	1/22	147

NOTE: Tree species are identified by their initials (see Table 1). Data pooled for branch clipping, intercept flight traps, and pyrethrum knockdown.

[a] Numbers used in the plots of the ordination diagrams (see Figures 3 and 4).

[b] Number of morphospecies/number of individuals.

APPENDIX 3

NUMBER OF INDIVIDUALS OF NONHERBIVORE INSECTS COLLECTED ON EACH TREE SPECIES, DETAILED FOR THE MOST COMMON INSECT FAMILY

INSECT TAXA	Et	Cc	Pp	Fn	Pa	Ca	Cb	Am	Md	Cd	TOTAL
Blattodea											
56. Blattellidae	31	35	28	108	69	79	2	16	34	30	432
Coleoptera											
57. Anthicidae	35	25	6	42	5	6	0	109	10	2	240
58. Anthribidae	46	10	23	26	18	39	4	78	29	36	309
59. Biphyllidae	1	0	11	0	1	0	34	0	0	4	51
60. Brentidae	0	0	0	6	1	2	31	2	4	1	47
61. Buprestidae	3	4	0	26	6	8	1	0	1	3	52
62. Cantharidae	8	250	11	98	12	24	12	9	10	5	439
63. Cerambycidae	56	17	29	98	31	22	9	88	34	18	402
64. Cleridae	41	5	20	53	18	25	11	53	44	30	300
65. Coccinellidae	60	28	47	201	125	65	32	95	57	48	758
66. Corylophidae	31	13	46	54	70	14	45	45	108	20	446
67. Cucujidae	6	1	6	6	2	1	4	8	10	3	47
68. Histeridae	0	6	12	6	8	2	0	9	3	2	48
69. Laemophloidae	4	0	4	3	1	1	1	13	3	1	31
70. Lathridiidae	1	4	12	2	3	14	15	5	12	6	74
71. Mordellidae	22	20	14	8	7	20	3	6	23	8	131
72. Mycetophagidae	26	6	38	9	12	10	1	30	18	18	168
73. Nitidulidae	10	1	23	5	8	3	1	5	14	2	72
74. Platypodidae	2	3	12	5	2	8	137	3	6	9	187
75. Pselaphidae	0	1	5	3	1	1	22	0	3	3	39
76. Scolytidae	36	31	74	53	66	96	84	82	87	31	640
77. Staphylinidae	25	288	117	23	52	191	54	28	44	23	845
78. Tenebrionidae	59	15	31	102	6	25	5	55	35	28	361
Collembola											
79. Entomobryidae	18	371	345	351	141	127	29	218	69	42	1,711
Dermaptera											
80. Forficularidae	11	4	35	28	7	7	29	6	2	15	144
Diptera											
81. Cecidomyiidae	112	413	350	123	630	597	179	135	206	266	3,011
82. Ceratopogonidae	47	98	73	46	34	93	22	215	182	70	880
83. Chironomidae	65	26	135	62	37	58	179	108	89	37	796
84. Dolichopodidae	54	18	17	44	15	37	140	42	13	11	391
85. Drosophilidae	0	4	11	2	3	6	1	3	0	0	30
86. Empididae	6	2	11	4	4	16	34	9	11	13	110
87. Lauxaniidae	0	1	3	0	2	0	10	0	0	0	16
88. Mycetophilidae	31	30	72	66	16	22	75	47	21	31	411
89. Phoridae	18	9	28	11	13	23	29	66	17	27	241
90. Psychodidae	88	231	184	58	102	108	52	249	134	202	1,408
91. Sciaridae	236	163	215	393	299	134	338	400	475	397	3,050
92. Stratiomyidae	14	16	6	7	4	66	5	15	12	24	169
93. Syrphidae	2	12	1	1	2	1	0	2	2	1	24
Hemiptera											
94. Anthocoridae	7	3	23	6	15	8	7	11	29	9	118
95. Enicocephalidae	0	1	1	2	0	1	17	0	0	2	24
96. Miridae	219	77	86	147	504	193	35	147	247	350	2,005
97. Nabiidae	31	0	4	32	15	20	3	11	15	9	140
Hymenoptera											
98. Braconidae	28	28	69	41	17	103	41	43	40	45	455
99. Encyrtidae	71	33	34	22	17	38	3	83	50	26	377
100. Eulophidae	5	16	31	0	15	19	8	7	4	35	140

APPENDIX 3 (continued)

INSECT TAXA	Et	Cc	Pp	Fn	Pa	Ca	Cb	Am	Md	Cd	TOTAL
101. Eupelmidae	17	10	8	21	11	19	1	16	13	22	138
102. Formicidae	1,503	1,438	1,015	1,704	1,315	2,174	53	843	1,098	1,156	12,299
103. Ichneumonidae	9	29	18	11	0	34	7	10	9	17	144
104. Pteromalidae	15	18	16	14	7	73	5	28	10	13	199
105. Scelionidae	36	30	35	11	45	35	5	30	39	44	310
Mantodea											
106. Mantidae	3	13	1	7	5	9	1	0	3	3	45
Neuroptera											
107. Chrysopidae	6	1	2	9	3	21	0	1	13	12	68
108. Coniopterygidae	4	1	1	1	1	7	6	12	11	5	49
109. Hemerobiidae	103	26	70	16	11	58	6	17	34	60	401
110. Mantispidae	1	3	0	3	0	12	0	3	5	2	29
Thysanoptera											
111. Phlaeothripidae	78	24	78	43	23	39	9	83	503	22	902

NOTE: Tree species are identified by their initials (see Table 1). Data pooled for branch clipping, intercept flight traps, and pyrethrum knockdown.